

BEYOND SIZE: MATRIX PROJECTION MODELS FOR POPULATIONS WHERE SIZE IS AN INCOMPLETE DESCRIPTOR

CATHERINE A. PFISTER^{1,3} AND MEI WANG²

¹Department of Ecology and Evolution, 1101 E. 57th Street, University of Chicago, Chicago, Illinois 60637 USA

²Department of Statistics, University of Chicago, Chicago, Illinois 60637 USA

Abstract. Size-based matrix models have been an important analytical tool in the study of populations. Although size can be an important variable in determining demographic parameters such as survivorship, growth, and reproduction, other factors such as genetic variation and access to resources can play key roles. We determined that size was not the only state variable that explained the survivorship, reproduction and future growth of the annual kelp, *Alaria nana*. *A. nana* shows persistent differences among individuals in growth (growth autocorrelation) that could be characterized with a negative residual (relatively poor growth) or positive residual (relatively good growth) from the relationship between size and growth. In two separate years of demographic study, we show that, during good growth conditions, growth autocorrelation is relatively strong, while poorer growth conditions associated with the 1997 El Niño event resulted in less consistency among individuals in growth state. To quantitatively describe this population, we used a size based matrix model with an added state to reflect previous growth status. We show that a matrix projection model with growth state better captures the size structure of a natural population of *A. nana* and the fate of individuals than one that uses only size. Without growth state, a size-based model underestimates the number of individuals that get large and thus the potential growth rate of the population. When we used our model to approximate among-generations pattern, and included a loop analysis algorithm, we found that fast growth to the largest size class contributed greatly to population growth in the relatively good year but that there were not such obvious benefits to getting large in the El Niño year. The size-based model with growth state that we present here is general and applicable to any species where persistent individual differences in performance violate the first-order Markov assumption of stage- or size-based matrix models.

Key words: demographic stochasticity; growth autocorrelation; kelp; matrix model; seaweed.

INTRODUCTION

Models structured by age, size, or stage are often used to describe the demography and project the population growth rate of plants and animals (Tuljapourkar and Caswell 1997, Caswell 2001). Because many organisms cannot be aged and many ecological factors are size dependent, models that use size as a state variable are especially useful, and include partial differential equations (de Roos et al. 1992, McCauley et al. 1996), integral projection models (Easterling et al. 2000), and matrix projection models (Caswell 2001). Matrix projection models are especially commonly used in ecology due to their relative ease of computation and the established methods for estimating sensitivities and elasticities. Although matrix models can and have been modified to be multistate (Caswell 2001), there are numerous examples of size-based matrix models in the literature, where the assumption is made that size as a state is sufficient to explain the demography of individuals. Matrix models share an

assumption common to all Markov models that state at time $t + 1$ is dependent only on the previous state at time t . Thus, size-based matrix models assume that the fates of individuals depend only on their current size. There are presumably many instances when this assumption is violated, because individuals of an identical size may have different fates depending upon their resource environment or their susceptibility to disturbance. For example, individuals within a population may experience both good and poor resource environments with respect to nutrients, light (Schmitt et al. 1986) or prey resources (Palmer 1984, Pfister and Peacor 2003). Inequities among individuals may be expressed in terms of growth or reproduction differences that are independent of size. In a species of kelp and a predatory gastropod, Pfister and Stevens (2002) expressed persistent differences in growth that were independent of size as “growth autocorrelation.” Growth autocorrelation was quantified as a positive correlation through time in residuals from a size vs. growth regression. The presence of growth autocorrelation within a population caused a strictly size-based matrix projection model to predict inaccurately the number of individuals in a population, including their size distribution (Pfister and Stevens 2003). In general, growth

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³ E-mail: cpfister@uchicago.edu

autocorrelation within a population leads to a greater disparity in the size distribution of individuals than a population without it and it generates some individuals who become large because they enjoy persistently high growth rates relative to others in the population. Our recognition that the Markov assumption is often violated in natural populations when size is used as the only state and there are heterogeneous fates of individuals motivated us to try to incorporate a "growth state" into matrix model framework. We ask if the addition of a state describing growth provided a more accurate projection of the population, and how it affected elasticities of different sizes to population growth rate.

We analyzed the demography of an intertidal kelp, *Alaria nana*, a species that has been demonstrated to show strong growth autocorrelation (Pfister and Stevens 2002) as well as size-related demographic rates (Pfister 1992). Although the precise mechanism underlying growth autocorrelation in *A. nana* is unknown, the strong potential for individuals to have differential access to light resources in plants (e.g., Schmitt et al. 1986, Dean et al. 1989, Reed 1990) may underly persistent growth differences. Our goal was to develop a matrix model approach that allowed individual fate to be determined by both size and growth information. Although growth rates and size are continuous variables, we used a structured matrix model because of the ease of use and potential application to multiple taxa. Problems can certainly arise when a usually continuous indicator of fate is broken down into discrete categories (Easterling et al. 2000); however, describing a population using models with several continuous state variables can rapidly lead to an analytical model that is not readily solved. Thus, as a first approach to the problem of modeling populations where growth history is important, we asked how the inclusion of growth performance as a state variable affected matrix projection model descriptors of *A. nana*.

We show that when we used a model that incorporated a new state that reflects either persistently good or poor growth, it yielded a superior fit to predicting plant fates and sizes than one that considered only size as a state. Our model with both growth and size as states also results in different elasticity estimates for a given size class. Our analysis of data for this annual kelp in two different years also suggests that the need to incorporate this state was greater for plants during a favorable year for growth where plant fates that were determined relatively early were rarely altered during their lifetime. Finally, we use a new loop analysis algorithm (L. Sun and M. Wang, *unpublished manuscript*) to show the consequences to population growth of different individual growth trajectories in the two years when environmental conditions differed.

STUDY SYSTEM

We studied the demography of *Alaria nana* on Tatoosh Island in Washington state (48°24' N, 124°44'

W), in both 1997 and 2001. *A. nana* occupies mid intertidal rocky intertidal sites, often colonizing patches of relatively bare space (Paine and Levin 1981). Sporophytes, the conspicuous diploid stage of kelp, become macroscopic in the late winter or early spring, grow throughout the summer, and then are usually ripped from the substrate by fall and winter storms. *A. nana* has an annual life cycle, although some individuals have been observed to survive through the winter into a second year. Although *Alaria* has specialized reproductive structures (sporophylls) that can contribute substantially to plant mass, the area of vegetative tissue is the primary determinant of frond growth (Pfister 1992). Sporophylls are borne at the base of the plant and develop spores as the growing season advances.

The two years of the study were characterized by very different oceanographic conditions for coastal seaweeds: 1997 was an El Niño year and mean monthly sea surface temperatures recorded near the study site (48° N, 124° W) were as much as 3.6°C greater in 1997 than 2001 (*data available online*).⁴ Similarly, indices of upwelling for the region indicated decreased upwelling during 1997 compared with 2001.

DEMOGRAPHIC DATA FOR *A. NANA*

Methods

From May through September in both 1997 and 2001, the pattern of growth, survivorship, and reproduction was studied in *A. nana* on Tatoosh Island. In 1997, a cohort of 215 plants was tagged on 7 May, while 224 plants were tagged on 23 May of 2001. Plants were individually identified with a numbered Floy tag (Floy Tag and Manufacturing, Seattle, Washington, USA) tied with fly-fishing backing line around the base of the stipe near the holdfast. Every two weeks (coincident with low tide), the frond length and width were measured and the length and reproductive status (spores present or absent) of each sporophyll was recorded. In 2001, sporophyll measurements were done less frequently (4–6 wk apart), due to time constraints. Sporophyll mass was estimated from a regression of sporophyll length to dry mass that was estimated separately for spore-bearing and non-spore-bearing sporophylls (Pfister 1992). We referred to this estimate of the mass of tissue committed to reproductive function as "reproductive investment," consistent with Pfister (1992). A one-eighth inch (~0.3 cm) office hole punch was used to put a hole in the base of the frond in the meristematic region (at 3–5 cm above the frond and stipe intersection). The linear distance this hole moved over a 2-wk interval was multiplied by the frond width at the beginning of the interval to yield an estimate of frond growth in area that was used for all estimates of growth. Kelp size was estimated as the frond length multiplied by the frond width. Due to herbivore- or wave-induced tissue loss, it was possible for kelp to

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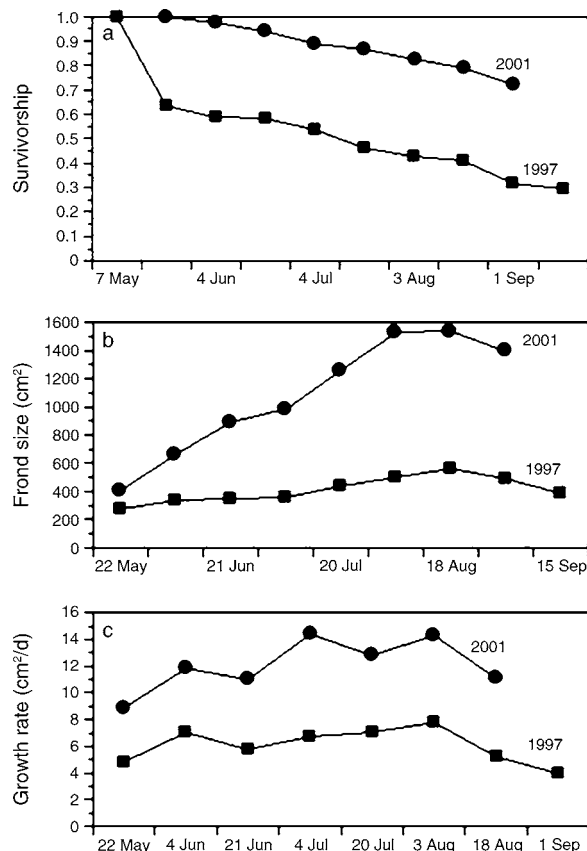


FIG. 1. (a) Survivorship, (b) size, and (c) growth of *Alaria nana* in 1997 and 2001, where survivorship is estimated from the beginning of the censusing in May.

have net growth from one interval to the next, but decrease in size.

We quantified growth and reproductive autocorrelation in *A. nana* and tested whether they were important to understanding the fate of individuals in natural populations. At every interval that *A. nana* was censused, we characterized plants as having either above or below average growth for its size. Using the sequential estimates of growth and reproduction in both

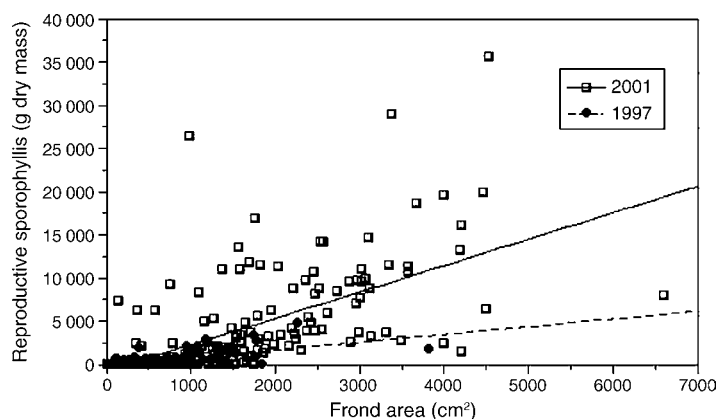
years, the strength of autocorrelation was estimated from the correlation of residuals at time t and residuals at time $t + 1$. Those with a positive residual were doing better than the average individual of their size, while those that had a negative residual were doing relatively worse. We used the sign of the growth residual as a growth status indicator. We tested how well size and the sign of the growth residual explained variability in survivorship and reproduction for two different years of data for *A. nana*, in 1997 ($n = 215$) and 2001 ($n = 224$). At every 2-wk interval throughout the study period, we used a logistic regression with size at time t (as frond area, in cm^2) and the sign of the growth residual from $t - 1$ to t (either positive or negative) as independent variables and either survivorship or the presence or absence of reproductive sporophylls at time t as the dependent variable. We compared a model with both state variables with one that only used size to ask if the inclusion of growth residuals significantly improved the prediction of individual fates. In the case of reproductive autocorrelation, some dependence among census intervals may be expected because, while sporophylls are continually forming and sloughing, some sporophylls from previous censuses may persist.

RESULTS

A. nana individuals in 1997 were characterized by poorer growth, smaller size and lower survivorship than those for 2001 (Fig. 1). Reproductive investment was greater in 2001 than 1997 both in absolute terms and for any given frond area (Fig. 2). Thus, by all metrics, 2001 was a better year for *A. nana* than 1997. In addition to the increased sea surface temperature and possibility of decreased upwelling during 1997, an early desiccation event (during the interval beginning on 7 May) resulted in important among year differences that are explored in the modeling below.

Autocorrelation in growth and reproduction was a strong feature of the biology of *A. nana* in both years of study. The estimates of growth autocorrelation ranged from 0.402 to 0.621 during 1997, with a mean of 0.478. These values are the correlation coefficient

FIG. 2. The relationship between *Alaria* reproductive investment (estimated as g dry mass of reproductive sporophylls) and size in July of 1997 and 2001. Slopes were not homogeneous ($F_{1,353} = 20.0$, $P < 0.001$). Regression coefficients were 0.89 in 1997 and 3.05 in 2001 and were statistically significant ($P < 0.001$; $r^2 = 0.522$ and 0.429, respectively).



between the residuals at time t and the residuals at time $t + 1$. Growth autocorrelation estimates were similar in 2001, ranging from 0.370 to 0.646 with a mean of 0.539. All estimates of growth autocorrelation were statistically significant. The analysis of autocorrelation in reproductive investment yielded concordant results. In 1997, the correlations between residuals from a size vs. reproductive investment regression at time t and $t + 1$ ranged from 0.351 to 0.817 and a mean of 0.573. For the three intervals where we could estimate reproductive autocorrelation in 2001, two of them were statistically significant.

In both years, a logistic regression model that used both size and the sign of the growth residual as independent variables always provided a better fit to the data on survivorship than a model with size alone. Likelihood ratio tests for all intervals in both years of study showed that a model with growth residuals and size improved the fit of the model to the data compared with a model with size alone ($P < 0.001$ for all 13 intervals).

In addition to accounting for some of variation in survivorship, growth residuals were an important explanatory variable for the presence of reproductive sporophylls in *A. nana* ($P < 0.001$ for nine of 10 intervals). For the intervals during June and beyond, when *A. nana* sporophylls began to bear spores, there was only one interval in 1997 when size alone provided as good of a fit to the data as size and growth residuals. Thus, despite the relatively crude designation of individual kelp into either positive or negative growth residuals, this distinction was an important one to explaining the fate of individuals in the field.

MODELING THE *A. NANA* POPULATION

Methods

The presence of autocorrelation in growth and reproduction and the importance of growth residuals in explaining the fate of individual *A. nana* motivated a model that included information about growth beyond that which is included in a strictly size-based model. Given the appropriateness of matrix projection models for size-structured populations and their ease in understanding how different components contribute to population growth rate via elasticities, we chose to build on a size-based matrix model for the *A. nana* population. We hypothesized that a size structured matrix model that was modified to include a state for growth performance would be a more accurate descriptor for *A. nana* than a strictly size-based model.

There are two time scales of analysis for *A. nana*: within and among generations. Our within-generation analysis focuses on growth and survivorship during the growing season and how these determine the size structure of the population and the size and number of reproductive adults. We used an among generation analysis to ask how different components of the life cycle and different loops contributed to population growth.

To address the usefulness of a growth state on a within generation scale, we asked how well a matrix projection model with size only fit the cohort data vs. one where a growth state was incorporated. We divided the *A. nana* population into three size classes, where size class 1 was ≤ 600 cm², size class 2 was 601–1200 cm², and size class 3 were those individuals > 1200 cm². These delineations were made based on the observation that individuals in the first size class rarely reproduced. We first considered a matrix model where size was the only state variable:

$$\begin{bmatrix} s_1(1 - g_1) & F_2 & F_3 \\ s_1g_1 & s_2(1 - g_2) & 0 \\ 0 & s_2g_2 & s_3 \end{bmatrix} \quad (1)$$

where s_i is the probability of survival of size class i , g_i is the probability that an individual in size class i grows to the next size class. Note that g_i terms are based strictly on changes in frond area and are not based on the hole punch growth data that were used to designate growth state. Although it was possible for individuals to lose enough tissue that they regressed to a previous size class, this was rare and we did not include it in our matrices. Fecundity terms (F_i) were set to zero for the within generation analysis.

We next added growth state to the model, using the simplest case where individual growth was either low or high (see Eq. 2 at bottom of page). We defined $p_{LH,i}$ to be the probability that a size i slow-growing individual becomes a fast-growing one, and $p_{HL,i}$ to define the reverse. Likewise, $p_{LL,i}$ and $p_{HH,i}$ are the probabilities of remaining in either a low or high growth state, respectively, and $p_{LL,i} = 1 - p_{LH,i}$ and $p_{HH,i} = 1 - p_{HL,i}$. We used the sign of the residual from a regression of the size at time t vs. growth from t to $t + 1$ as a growth status indicator at each census. A slow grower was defined by a negative residual while a positive residual designated a fast grower. In this way we were able to estimate the transition probabilities among sizes and among growth states. Fecundity terms were again set to zero.

$$\begin{bmatrix} s_{L,1}(1 - g_{L,1})p_{LL,1} & s_{H,1}(1 - g_{H,1})p_{HL,1} & F_{LL,2} & F_{HL,2} & F_{LL,3} & F_{HL,3} \\ s_{L,1}(1 - g_{L,1})p_{LH,1} & s_{H,1}(1 - g_{H,1})p_{HH,1} & F_{LH,2} & F_{HH,2} & F_{LH,3} & F_{HH,3} \\ s_{L,1}g_{L,1}p_{LL,1} & s_{H,1}g_{H,1}p_{HL,1} & s_{L,2}(1 - g_{L,2})p_{LL,2} & s_{H,2}(1 - g_{H,2})p_{HL,2} & 0 & 0 \\ s_{L,1}g_{L,1}p_{LH,1} & s_{H,1}g_{H,1}p_{HH,1} & s_{L,2}(1 - g_{L,2})p_{LH,2} & s_{H,2}(1 - g_{H,2})p_{HH,2} & 0 & 0 \\ 0 & 0 & s_{L,2}g_{L,2}p_{LL,2} & s_{H,2}g_{H,2}p_{HL,2} & s_{L,3}p_{LL,3} & s_{H,3}p_{HL,3} \\ 0 & 0 & s_{L,2}g_{L,2}p_{LH,2} & s_{H,2}g_{H,2}p_{HH,2} & s_{L,3}p_{LH,3} & s_{H,3}p_{HH,3} \end{bmatrix} \quad (2)$$

For both Eqs. 1 and 2, parameters were estimated from two different years of study, 1997 and 2001. Within each of those years, we had either nine (1997) or seven (2001) intervals of two weeks each where parameters were estimated. We first estimated mean matrix parameters using each interval during which we had data and weighting the contribution of that interval for the number of plants that were sampled. The number of plants providing information in any interval could vary due not only to death, but also the missing growth information if a “growth hole punch” was missing or difficult to interpret.

In order to ask whether a six-state model with growth status was justified over a three-state model (with size as the only state), we also generated maximum likelihood estimates of the parameters in Eqs. 1 and 2, using a multinomial probability model. For these estimates, the final state of an individual (including death) was based on its initial state. Although this approach allowed us to use likelihoods and test whether the more parameter-rich six-state model was favored by AIC when compared to the actual size structured data (e.g., Burnham and Anderson 1998), the disadvantage of this parameter estimation technique was that we imputed some data to have a consistent count of plants through time. Thus, for any interval where we were missing growth information, we guessed the growth residual based on the pattern of growth residuals either prior to or after this interval. We explored the effect of imputed data on our results by removing plants from the analysis when their were missing data and re-estimating parameters with MLE. We then compared the MLE method of parameter estimation for a within generation matrix model with our simple estimate of weighted means.

We examined the implications of among generation time scales and the contributions of different matrix entries to population growth rate of *A. nana*. We again used Eqs. 1 and 2, this time with F_i terms as estimates of reproductive investment (or estimated sporophyll mass) for each individual. In the case of F_i terms in Eq. 2, we assumed that individuals in either state produced an equal number of low and high growth offspring. Due to the microscopic size of the spores and their tremendous potential for dispersal (Kusumo and Druehl 2000), it is impossible to know the actual number of offspring produced by any individual. However, we estimated sporophyll mass, found it to be positively correlated with plant size, and scaled our F_i terms with size such that the population would be stable ($\lambda = 1$).

Our primary goal in using matrix models for an among generation analysis was not to describe a long term population growth rate (λ) from only a single year of data. Rather, our motivation was to explore how elasticities were assigned to individual matrix transitions and loops in our matrices, thus providing a link between demographic events and their relative effect on population growth rate in different years. For an

annual species such as *Alaria*, a fully parameterized annual matrix model would be the product of both the summer growth events and reproduction and recruitment in the fall and winter. However, such a composite matrix is impossible for us to parameterize precisely, due to a lack of information on reproduction and recruitment. Thus, the matrix structure we used was the May through September matrix (e.g., Eqs. 1 and 2) with fecundity terms added in the first row, and with s_3 and p_3 set to zero because no individuals start as size 3. We scaled fecundity to have $\lambda = 1$; the resultant matrix was amenable to comparative elasticity analysis and loop analysis. We estimated all s_1 , s_2 , g_1 , and g_2 based on survivorship and growth from the beginning of the spring to the fall. Thus, individuals that started the season in the size class 1 could grow to either size class 2 or 3 by September, given that they survived. Estimates of growth state transitions (all p_2 and p_3) were based on the predominant sign of the growth residuals in the first half of the growing season (May through mid July) compared with the second half of the growing season (mid July through September). For example, an individual *A. nana* that started in size class 1 and had positive residuals in a majority of the intervals throughout the growing season would be classified in the $p_{HH,1}$ parameter. In several cases, the sign of the growth residuals for individual *A. nana* were highly changeable, and these individuals could not be classified ($n = 15$ in each year).

In addition to using elasticities of individual matrix entries to infer potential effects on population growth, we also used loop analysis to understand the consequences to λ of different individual fates, including the effects that fecundity has in the “life cycle loop” that an individual plant may follow. Loop analysis uses the structure of the life history described by a matrix model to incorporate joint effects of growth, survivorship and reproduction on λ (van Groenendael et al. 1994, Wardle 1998; L. Sun and M. Wang, *unpublished manuscript*). Fig. 3 shows the life cycle diagram for the model in Eq. 2 from which we traced individual loops for *A. nana*. We were particularly interested in whether loops incorporating different growth states made differential contributions to λ and whether these contributions differed in the two years. We decomposed our 6×6 matrix with growth state (Eq. 2) using a searching algorithm that sequentially extracts individual life cycle loops. Our procedure, which is almost the reverse of that used in the Spanning Tree Approach underlying van Groenendael et al. (1994) and Wardle (1998), uses a unique edge elasticity to designate the loop elasticity (L. Sun and M. Wang, *unpublished manuscript*). Although there are 23 independent loops for Eq. 2, we were particularly interested in loops that quantified the consequences of being a slow or fast grower in each year where the conditions markedly differed. We were also able to explore the effects of switching from slow to fast growth. We note that although we report quantitative

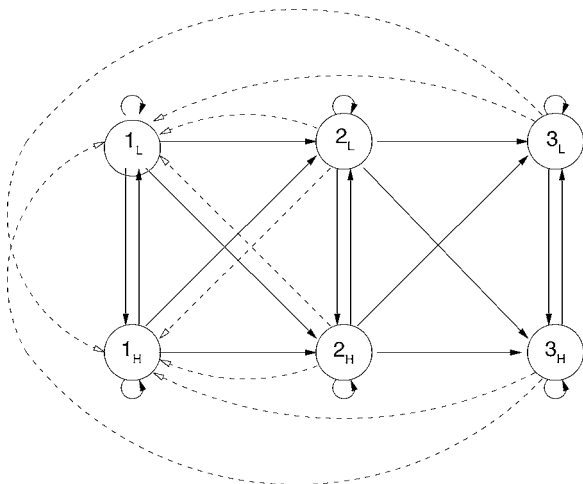


FIG. 3. A life cycle diagram (and the basis for the loop analysis) for the potential states (three size classes and two growth rates [low, L; high, H]) of *A. nana* from a model based on Eq. 2.

estimates for elasticities and loops, we interpret them qualitatively because our among generation matrix is not a continuous population projection model as is usually formulated for perennial populations.

Results

Not surprisingly, matrix model parameter estimates showed higher growth, survivorship, and fecundity in 2001 compared with 1997 (Table 1 and Fig. 4). Analysis of parameter estimates for Eq. 2 show that using growth residuals as a growth status indicator had a large effect on the estimation of g_i and p_i , especially in 2001 (Table 2). The survivorship and fecundity terms were less affected by a characterization of growth state. Note that $p_{HL,i}$ often differs from $p_{LH,i}$ due not only to differences in the individual fates in each growth state,

but also due to the disparities in g_i and occasional interval where growth data were missing for plants in some categories.

The matrix projection models without fecundity terms represent the average transition probabilities during the annual growing season and can be used in a within generation analysis where the size structure of the population is projected. Although we show only the parameter estimates based on weighted means for Eqs. 1 and 2 (Table 1), the maximum likelihood estimates (MLE) of parameters based on imputed data in a multinomial probability model were very similar. MLE parameter estimates for Eq. (2), where growth state is included in the model, were more consistent with the data than the strictly size based model shown in Eq. 1 for both years of analysis. AIC estimates for the six-state model were 835 in 1997 compared with 1634 for the size only model; in 2001, AIC estimates were 752 and 1401, respectively. Thus, despite the greater number of parameters, a model with six states is a superior fit to the data on size structure. When we removed all imputed data from our analyses and re-estimated the MLE, a six-state model with growth was still favored with AIC (1997, 754 vs. 1003; 2001, 709 vs. 1079 for six-state and three-size only models, respectively), despite the relatively lower sample size.

When we used the within generation matrix projection models in a projection of size structure through a growing season, Eq. 2, where growth state is included in the model, was more consistent with the data than the strictly size based model (Eq. 1), especially in 2001 (Fig. 5). In 2001, a period during which growth was highly consistent among individuals (Fig. 4), a strictly size-based model especially underestimated both the total number of individuals in the population and those in the largest size class.

When we parameterized a matrix model for among generations and included fecundity terms, there were

TABLE 1. Matrix model transition elements for (a) a three-size-class within-generation model (Eq. 1) and (b) a size-based model with growth state added.

	1997	2001
a) Three-size-class model (Eq. 1):	$\begin{bmatrix} 0.8105 & 0 & 0 \\ 0.0445 & 0.6039 & 0 \\ 0 & 0.3181 & 0.9160 \end{bmatrix}$	$\begin{bmatrix} 0.7321 & 0 & 0 \\ 0.1729 & 0.5888 & 0 \\ 0 & 0.3892 & 0.9520 \end{bmatrix}$
b) Three-size-class model with growth state added (Eq. 2):	$\begin{bmatrix} 0.6380 & 0.2121 & 0 & 0 & 0 & 0 \\ 0.1884 & 0.5194 & 0 & 0 & 0 & 0 \\ 0.0197 & 0.0413 & 0.3418 & 0.2539 & 0 & 0 \\ 0.0058 & 0.1011 & 0.2288 & 0.3311 & 0 & 0 \\ 0 & 0 & 0.1865 & 0.1228 & 0.6035 & 0.3781 \\ 0 & 0 & 0.1248 & 0.1602 & 0.2945 & 0.5509 \end{bmatrix}$	$\begin{bmatrix} 0.7001 & 0.1154 & 0 & 0 & 0 & 0 \\ 0.1111 & 0.3909 & 0 & 0 & 0 & 0 \\ 0.0973 & 0.1096 & 0.4700 & 0.1295 & 0 & 0 \\ 0.0154 & 0.3711 & 0.3005 & 0.3520 & 0 & 0 \\ 0 & 0 & 0.1333 & 0.1311 & 0.7292 & 0.2550 \\ 0 & 0 & 0.0852 & 0.3563 & 0.2278 & 0.7000 \end{bmatrix}$

Note: Models were parameterized separately for 1997 and 2001 and values in (b) are weighted means based on the parameter estimates in Fig. 4.

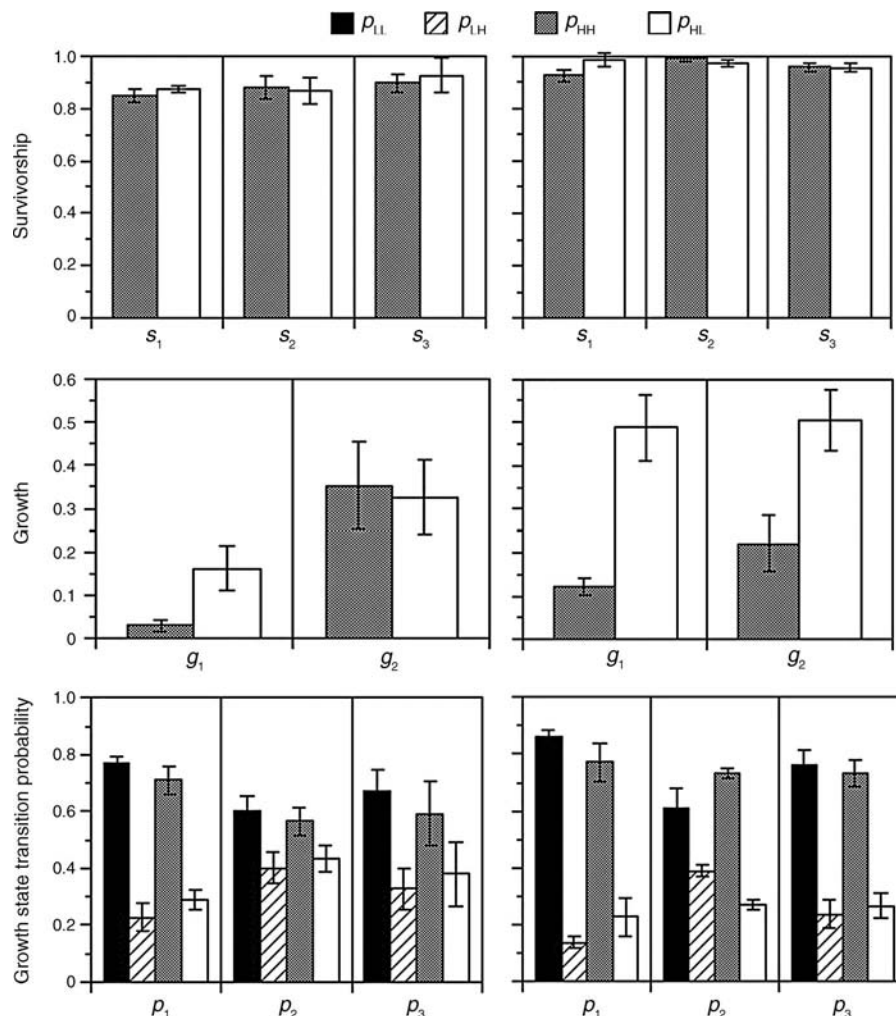


FIG. 4. Parameter estimates for 1997 (left column) and 2001 (right column) used for the within-generation matrix entries in Eq. 2. Values are means \pm SE of estimations every two weeks throughout the growing season. Means were weighted for the sample size available at each date. For a–d, the shaded bars represent low growth (those with negative growth residuals), and the open bars are the high growers (those with positive growth residuals); where s_1 , s_2 , and s_3 are the probability of survivorship for each two-week interval for individuals in size classes 1, 2, and 3, respectively; g_1 and g_2 are the probabilities of growing into size class 1 and 2, respectively; and p_1 , p_2 , and p_3 are the probabilities that individuals in each of size classes 1, 2, and 3 remained in their growth state.

marked patterns in the elasticities between the two years of study (Table 2). In the El Niño year of 1997, plants were smaller and grew and reproduced less and events in size class 1 had the greatest contribution to λ . In contrast, the relatively good growing conditions of 2001 revealed that more individuals grew from size class 1 to 3 and the elasticity of this transition for good growers was especially high. Reproduction of size class 3 plants also contributed greatly to population growth, especially in the instances where the largest individuals produced progeny that were high growers.

Loop analysis showed important similarities and differences among the two years of study. The loop that included consistently high growth always contributed more to λ than one that had constant poor growth (Table 3a vs. b). However, in a poor year such as 1997, there

was a relatively small elasticity for individuals that grew directly to size class 3, whereas the elasticity for this loop in 2001 was relatively high (Table 3c vs. d and e vs. f). Although the algorithm that we used avoids many of the problems of the spanning tree method, such as negative loops (L. Sun and M. Wang, *unpublished manuscript*), there are still certain loops that are difficult to isolate in the life cycle. Thus, a complete comparison of the effects of individuals switching between growth states in both years is difficult, but our analyses do reveal that the loop elasticities are relatively small in comparison with the greater contribution to λ made by loops of consistently high growth (Table 3g–i). Thus, consistently rapid growth, especially to size class 3, contributed greatly to the rate of population change in 2001.

TABLE 2. (a) Matrix model transition elements for a size-based model with growth state added (Eq. 2) and parameterized for among generations (yearly) and (b) the corresponding elasticities.

	1997						2001					
a) Transition elements:												
	0.6077	0.2020	0.4656	0.2782	0.5088	0.5163	0.3152	0.1040	0.2067	0.2171	0.5388	0.6682
	0.2460	0.3124	0.4656	0.2782	0.5088	0.5163	0.1732	0.1112	0.2067	0.2171	0.5388	0.6682
	0.0185	0.0442	0.1814	0.1361	0	0	0.1225	0.0824	0.0349	0.0293	0	0
	0.0050	0.0883	0.0493	0.2722	0	0	0.0484	0.1011	0.0138	0.0359	0	0
	0.0292	0.1177	0.3629	0.1361	0	0	0.0967	0.2662	0.4189	0.3510	0	0
	0.0079	0.2354	0.0986	0.2722	0	0	0.0382	0.3266	0.1656	0.4307	0	0
b) Elasticities:												
	0.2276	0.0544	0.0135	0.0103	0.0295	0.0408	0.0778	0.0222	0.0104	0.0077	0.0613	0.0684
	0.1150	0.1050	0.0168	0.0129	0.0368	0.0509	0.0609	0.0338	0.0148	0.0109	0.0872	0.0973
	0.0140	0.0241	0.0107	0.0102	0	0	0.0417	0.0243	0.0024	0.0014	0	0
	0.0035	0.0445	0.0027	0.0189	0	0	0.0212	0.0383	0.0012	0.0023	0	0
	0.0125	0.0361	0.0120	0.0057	0	0	0.0311	0.0739	0.0275	0.0161	0	0
	0.0034	0.0733	0.0033	0.0116	0	0	0.0152	0.1125	0.0135	0.0246	0	0

Notes: Boldface type indicates the five greatest elasticities. Fecundity terms were estimated based on $\lambda = 1$.

DISCUSSION

Although growth rates are a continuum from poor to good in *A. nana* (Pfister and Stevens 2002), the simple division of the population into those with “low” vs. “high” growth based on residuals from a size vs. growth relationship explained a remarkable amount of the variation in reproduction and survivorship. Note that correlations of reproduction, growth and survivorship with size were also found for *A. nana*, and certainly motivated the use of a strictly size-based model. However, a model with only size as a state variable

would not have captured the variation in the population as well as a model with both size and growth as states. A size-based matrix model without growth state (Eq. 1) underestimated the number of individuals in the large size class in 2001, a result consistent with Pfister and Stevens (2003). In contrast, a model with growth state (Eq. 2) more accurately described the size dynamics of a cohort of *A. nana* and better captured the phenomenon of individuals becoming large quickly through autocorrelation in growth. When we used a model selection criterion that accounts for increased

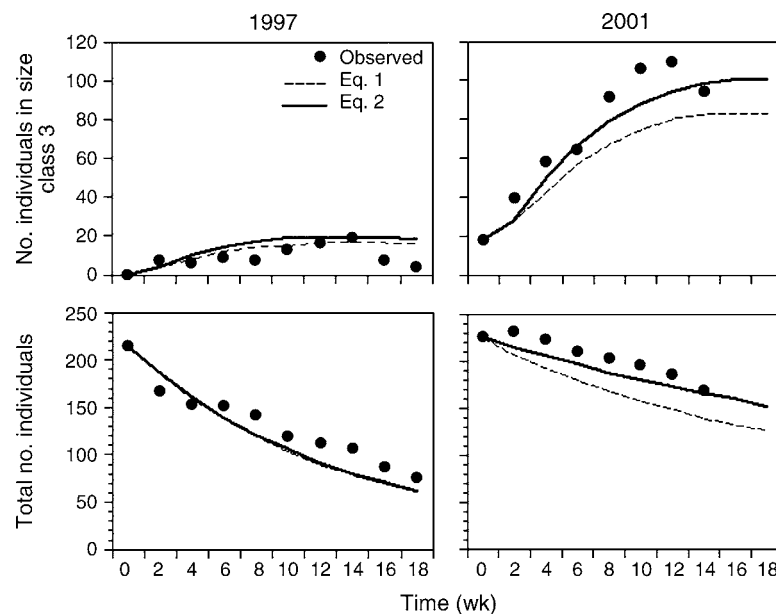


FIG. 5. A comparison of the within-generation projections of Eq. 1 (dashed line) and Eq. 2 (solid line) with the observed size distribution data during the season of growth (solid circles). The top two panels show the number of individuals in the largest size class only, while the bottom two panels show the total number of individuals.

TABLE 3. The loop elasticities for the life cycle loops of greatest interest to the comparison of high (H) vs. low (L) growth and the consequences of switching growth state.

Life cycle loop	1997	2001
a) $1_L \rightarrow 2_L \rightarrow 3_L \rightarrow 1_L$	0.15	5.40
b) $1_H \rightarrow 2_H \rightarrow 3_H \rightarrow 1_H$	2.43	7.08
c) $1_L \rightarrow 2_L \rightarrow 1_L$	2.70	2.08
d) $1_L \rightarrow 3_L \rightarrow 1_L$	2.50	6.22
e) $1_H \rightarrow 2_H \rightarrow 1_H$	2.58	2.18
f) $1_H \rightarrow 3_H \rightarrow 1_H$	8.56	14.76
g) $1_L \rightarrow 2_H \rightarrow 3_H \rightarrow 1_L$	1.05	0.30
h) $1_H \rightarrow 2_L \rightarrow 3_L \rightarrow 1_H$	null	2.85
i) $1_L \rightarrow 2_L \rightarrow 3_H \rightarrow 1_L$	null	3.99
j) $1_H \rightarrow 2_H \rightarrow 3_L \rightarrow 1_H$	null	1.14

Notes: The loops are taken from the life cycle graph (Fig. 3). Elasticities are expressed as a percentage.

parameters (AIC, e.g., Burnham and Anderson 1998), the more complex model with growth state was favored in both years. Although the multinomial probability models that we used clearly indicated that the fate of individual *Alaria* are not independent of growth state, there are further considerations, however, that may favor the use of a model with growth state in other taxa where growth autocorrelation may be weaker. First, the number of parameters may reasonably be reduced by the assumption of $p_{LL,i} = p_{HH,i}$, for some or all i . Similarly, the incidence of switching growth states may be similar in each direction, resulting in $p_{LH,i} = p_{HL,i}$. Second, the inclusion of growth state allows an estimation of the contribution of distinct individual paths and their contribution to population growth rate. Thus, the purpose of using a matrix model framework might not be to precisely replicate the size structure of the population, but to interpret the consequences of different growth states on population trajectories.

It is also important to note that the superior ability of a model with growth state to predict the number of individuals that become large is important in the context of population growth rate. A model without growth state predicts fewer large individuals, underestimating the reproductive capacity of the population and therefore the potential population growth rate. Even if the number of size classes is increased, a strictly size-based model still underestimates the number of large individuals (Pfister and Stevens 2003). Thus, if autocorrelation is important in a population and growth state is not explicitly modeled, then population growth rate will be underestimated because the individuals that become especially large and contribute disproportionately to population growth will be underestimated (Pfister and Stevens 2003). Similarly, Connor and White (1999) point out the importance that a relatively small number of individuals that contribute disproportionately to future generations have in ameliorating extinction risk.

The precise mechanisms underlying the patterns of autocorrelation in growth and reproductive investment in *A. nana* are unknown, but we present several hypotheses. As proposed by Huston and DeAngelis

(1987) for the pattern of size bimodality, mechanisms might be “inherent” or have an underlying genetic basis. There is currently no evidence for help that bears on this hypothesis, but trait differences in factors such as photosynthetic efficiency that differs among individuals would result in correlated performance. When we estimated autocorrelation over time periods greater than one two-week interval, the correlation could approach zero after three or four intervals, suggesting that “inherent” or genetic mechanisms do not underly the correlation (Diggle et al. 2002). Instead, mechanisms that are imposed by environmental variation may be driving the autocorrelation patterns we see. For example, the unequal distribution of light resources in kelp and terrestrial plants might result in individuals that are relatively suppressed or dominant (e.g., Schmitt et al. 1986). If differential access to resources is persistent, then autocorrelation should develop. To date, we cannot distinguish inherent from imposed mechanisms.

Patterns of growth that motivate a growth state in demographic models may be common across a variety of taxa. Growth autocorrelation was also demonstrated in a predatory marine snail (Pfister and Stevens 2002), but was not significant in a tide pool fish (Pfister and Stevens 2002) or a seastar (Carlson and Pfister 1999). However, the size structure of many terrestrial plants suggests an important role for growth state in their demography. For example, the documentation of dominant and suppressed individuals (Obeid et al. 1967, Harper 1977, Cousens and Hutchings 1983, Schmitt et al. 1986, 1987, Reed 1990) and the rapid development of size differences within cohorts suggests the role of more than strictly size-related processes (Lomnicki 1988, Pfister and Stevens 2002).

One of the striking features of the demography of *A. nana* is the difference among years. Individual reproduction, growth, and survivorship were markedly higher in 2001 than 1997 (Figs. 1, 2, and 4). Additionally, the growth state of plants during the better 2001 season was more stable, with a higher probability that individuals remained in their state (Table 1). Thus, better conditions for growth and survival in *A. nana* are associated with greater determinism in the fate of individuals. Although the causal mechanism driving the year to year differences are unknown, several possibilities exist, including the presence of an El Niño event during 1997 which was associated with higher water temperatures, lower nutrients (Wheeler and Hill 1999) and increased rain and storms (Allan and Komar 2002). Alternatively, or in combination, there may have been more protective coastal morning fog in 2001 during the hours and days that the intertidal *A. nana* was exposed to air (C. A. Pfister, *personal observation*). The net result was that plants shrank in size more in 1997 than 2001, as exemplified by a 16.2% vs. 6.4% chance of a transition from size class 3 to 2 in 1997 compared with 2001. We considered the possibility that

decreased growth in 1997 leads to an increased role of measurement error in estimations of growth and thus the perception that individuals are switching growth classes. If this were the case, then smaller plants (which grow less) should have lower estimates for $p_{LL,i}$ and $p_{HH,i}$, a pattern that is not supported by the data in either 1997 or 2001 (Fig. 4). Thus, the disparity in the predictability of plant fate in the two years appears to be related to environmental variation.

The marked differences in individual performance in the two years of study leads to several important issues in the analysis of population-level features. First, it is obvious that a model parameterized with data from one year will not describe well the population in the other year. Second, however, is that differences in the stability of growth state in 2001 increase the need to use a 6-state model. Additionally, the slowed growth of individuals in 1997, particularly out of size class 1 and into size class 2, results in an increased elasticity for size class 1 in the 1997 population. Thus, even though the delineation of growth state is weaker in the first size class in 1997, the elasticity for events in size class 1 are relatively higher in 1997 than 2001. The comparison among years also highlights the importance of large plants to population growth rate in a good year. The effects on λ of a disproportionate increase in fecundity with size in a good year (Fig. 2) is reflected in the loop analyses that demonstrate high loop elasticities for a rapid transition to size class 3 in 2001 compared with 1997 (Table 3).

Overall, loop analysis indicated the importance of fast growth to population growth rate, while showing little effect of the timing of switching growth states on population growth rate (Table 3). A fast growth loop always had a greater loop elasticity than slow growth or scenarios where switching occurred. The results from loop elasticities were fairly similar to the single element elasticities. A scenario that would have generated greater disparities between single element elasticities and loop analysis was the case where fecundities for large individuals differed more drastically as a function of growth state. Instead, these estimates were remarkably similar (Table 2b). Thus, although growth residuals were a good predictor of whether an individual would have reproductive sporophylls, larger plants did not show a great loss in reproductive function at the end of the growing season based on their growth status. These results parallel those from terrestrial plants that suggest that allocation to reproductive function is somewhat buffered and allocation to growth was more sensitive to extrinsic factors (*sensu* Reekie and Bazzaz 1987, Lubbers and Lechowicz 1989).

Although this modified matrix model with growth state included lacks a mechanistic basis and simply summarizes a pattern in the data, the model has the advantage that it is general and could be used across a variety of taxa where growth autocorrelation was demonstrated from preliminary demographic study. In

fact, for many of the size-based matrix projection models that have been published, the data probably exist to assess the importance of growth autocorrelation and to parameterize Eq. 2 if the inclusion of another state is justified by the data. The model that we use here is general enough that a variety of mechanisms that may underlie persistent individual differences could be included in a single growth state. For example, differences in prey choice that generated growth disparities (e.g., Palmer 1984) or variability in territory quality that resulted in disparities in breeding success (e.g., Hatch 1990) might be described with this simple addition of another state in a matrix model framework. Although there will be many instances where a single state variable such as age or size will be sufficient to describe a population, we offer a relatively simple model for the inclusion of an additional state that can capture the growth or performance history of individuals.

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